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Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change

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Abstract. As climates shift in space, tree species ranges are predicted to shift as well. While range shifts due to climate change have been typically modeled based on abiotic factors alone, interactions among species in diverse communities may alter these range dynamics by inhibiting or enhancing the establishment of propagules along the leading edge, or by increasing or decreasing tolerance to novel climates at the trailing edge. Here, we investigated how the rate of expansion at leading range margins, and contraction at trailing range margins of temperate tree species in response to both past and current climate change related to an important species interaction: whether temperate tree species associate with arbuscular (AM) or ectomycorrhizal (EM) fungal symbionts. Mycorrhizal symbioses can mediate plant stress tolerance, and lack of EM fungal mutualists has been linked to establishment failures of EM tree species in new ranges. We found no difference in rates of leading edge expansion between the two guilds. However, EM tree taxa showed reduced contraction at their trailing edge compared to AM taxa in response to both past and current climate change. Since the mycorrhizal guild of the dominant trees may affect ecosystem properties, differential range dynamics between these functional groups of trees may have consequences for the functioning of future forests.

Key words: *arbuscular mycorrhizae; eastern temperate forest; ectomycorrhizae; Forest Inventory and Analysis program; paleoecology; range shift.*

Introduction

At biogeographic scales, climate is one of the key factors determining tree species distributions (Whittaker 1975). Species ranges have shifted in response to past (Ordonez and Williams 2013) and contemporary (Parmesan and Yohe 2003, Angert et al. 2011, Chen et al. 2011, Buckley and Kingsolver 2012) climate change, expanding at the poleward (leading) edge and contracting at the equatorial (trailing) edge as climates warm. While species range shifts are typically predicted from abiotic variables, interactions among species may impact range dynamics by affecting dispersal and establishment (Svenning et al. 2014) and/or a species' tolerance to novel climates (Jones et al. 2008). Species interactions may affect range dynamics during climate warming through two main mechanisms: (1) by inhibiting or promoting range expansion into newly permissive areas beyond the leading range edge, and (2) by increasing or decreasing a species' ability to persist at its trailing range edge by broadening or narrowing its tolerance to novel climate conditions (Van der Putten et al. 2010, Svenning and Sandel 2013, Svenning et al. 2014). At the leading edge, escape from specialized natural enemies may promote establishment, which has been frequently found for exotic species (Liu and Stiling 2006) and recently documented in response to warming climates (Engelkes et al. 2008). However, competition by resident species (Urban et al. 2012) or lack of specialized mutualists (Nunez et al. 2009) may inhibit establishment in new areas. At the trailing edge, persistence as climates warm or dry may be reduced by increases in natural enemy or competitor populations or the loss of mutualists, while

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enhanced mutualisms or reductions in natural enemies or competitors may allow a species to tolerate a broader range of climates. For instance, host species may broaden their climate tolerance if they can adaptively switch symbionts as conditions change (Jones et al. 2008).

For plants, interactions with symbiotic root fungi play vital roles in nutrient acquisition, drought tolerance, and seedling establishment, and thus may be important mediators of climate responses (Kivlin et al. 2013). Tree species vary qualitatively in their symbiotic associations, typically forming connections with either arbuscular (AM) or ectomycorrhizal (EM) fungi (both can be formed in some families, e.g., the Salicaceae). AM associations are dominant in tropical forests, while EM associations are dominant in boreal forests; the two strategies coexist in temperate zones (Read and Perez-Moreno 2003, Phillips et al. 2013). The AM symbiosis is widespread geographically and phylogenetically, involving over 80% of extant terrestrial plant species (Smith and Read 2008). AM fungi act as extended root systems, and aid in the acquisition of poorly mobile soil nutrients (Smith and Read 2008). In contrast, the EM symbiosis evolved more recently, and multiple times in both plants and fungi (Smith and Read 2008). Only ~3% of plant species form EM symbioses, but these include ecologically and economically important canopy tree species such as pines, oaks, and hickories (Smith and Read 2008). EM fungi descend from saprotrophic fungi, and as such, some are able to acquire nutrients for their hosts directly from organic matter (Phillips et al. 2013). Understanding the future distribution of EM vs. AM tree species may prove important for accurately modeling the global carbon cycle, as the dominance of a mycorrhizal type has been linked to soil carbon dynamics (Averill et al. 2014).

Mycorrhizal symbioses may affect the rate at which tree ranges can track changing climates, if mismatches in the migration rates of trees and fungi inhibit tree establishment in new areas due to a lack of specialized mutualists. The ancient AM symbiosis is highly generalized and taxa are widely distributed; therefore, a lack of AM symbionts is unlikely to be a significant dispersal barrier (Pringle et al. 2009). However, EM fungi can vary from broadly generalized, to specialized on single plant families or even genera (Smith and Read 2008). The specificity of EM symbioses has been linked to colonization failures in EM trees exported to new areas (Nunez et al. 2009, Pringle et al. 2009). Isolated EM trees have also shown reduced EM fungal diversity compared to conspecifics growing in dense forests (Peay et al. 2010). Thus, the range expansion of EM trees may be slowed by an overall lack of EM fungi, or more subtly suffer from a lack of closely adapted, specialized fungal symbionts.

Mycorrhizal symbiosis may also affect the host's tolerance of novel climates. Colonization by either AM or EM fungi has been shown to increase drought tolerance of hosts relative to uncolonized plants through a combination of increased access to water and increased access to soil nutrients in dry soils (Kivlin et al. 2013). The higher taxonomic, morphological, and functional diversity (e.g., in nutrient acquisition strategies) of EM fungi may provide their hosts with a greater buffer against changing environmental conditions. This could be especially important in warming and/or drying conditions if hosts can adaptively switch their fungal symbionts to better match the new conditions as can occur in other host–symbiont relationships (Jones et al. 2008), although this phenomenon has not been investigated for the EM symbiosis to our knowledge. Perhaps more importantly, both AM and EM fungi can connect multiple hosts in common mycorrhizal networks (van der Heijden and Horton 2009, Booth and Hoeksema 2010, Bingham and Simard 2012). However, EM networks can connect hosts over much larger spatial scales, and have been documented to support seedlings in stressful conditions by transferring carbon, nutrients, and water from established adult trees (van der Heijden and Horton 2009, Courty et al. 2010). Evidence from AM networks has instead shown competition between seedlings and established plants in a linked network (Merrild et al. 2013).

To assess whether mycorrhizal type was associated with range expansion and/or contraction, we took advantage of two large datasets on past and current tree species distributions. First, we used estimates of range expansion and contraction for 18 North American tree genera during the end of the Younger Dryas (12 000–10 000 years BP), estimated from pollen records (Ordonez and Williams 2013). Secondly, we used the United States Forest Service Forest Inventory and Analysis (FIA) dataset to determine the geographic extent of seedlings vs. adult trees for sets of 97 (trailing edge) and 83 (leading edge) species using the methods of Zhu et al. (2012). Here, early stages of expansion at the leading edge would be evident by seedling range limits that were further north than adult tree range limits at the northern range edge. Evidence of trailing edge contraction would come from seedling southern range limits that occur at more northern latitudes than the adult trees, indicating recruitment failure along the southern range edge. If greater specialization in EM vs. AM symbioses limits establishment in new areas, we hypothesized that in both the historic and contemporary datasets AM trees would show greater rates of expansion relative to climate velocity at the leading edge. Additionally, if EM symbioses increase climate tolerances of hosts compared to AM associations, then we expect reduced rates of trailing edge contraction relative to climate velocity for EM species.

Methods

Data for biotic and climate velocities for 25 genera over the last 16 000 years were taken from Ordonez and Williams (2013). In brief, the authors used pollen

records from the NEOTOMA fossil pollen database (*available online*).[6] To determine biotic velocities for each 2000 year time period, the authors determined the latitude that defined the upper 95th or lower 5th percentile of occurrences in 0.5° longitudinal bands across the genus core distribution at the beginning and end of each time period. Climate velocities were measured as the spatial displacement of climate (the location of the closest climatic analog based on 12 temperature and precipitation variables) within longitudinal bands during the given time period. Here, we focus on range dynamics during the period of most rapid warming, 12 000–10 000 years BP (Ordonez and Williams 2013).

Estimates of contemporary range dynamics were derived from the United States Forest Service Forest Inventory and Analysis (FIA) data set using the methods of Zhu et al. (2012). This dataset integrates tree demographic responses to climate over several decades for most species. Latitudinal difference distributions (LDD) were calculated for the leading (and trailing) edge as the difference in the northern (southern) extent of seedling and the northern (southern) extent of adult tree observations. Because we analyzed trailing edge dynamics for species whose distributions extend beyond the FIA dataset, a set percentile cut-off determined solely by the information available in the FIA dataset could be misleading. Therefore, we used an alternative metric of range edges that was independent of range extent. We first determined the absolute minimum adult tree observation in a 1° longitudinal band, and then took the median latitude of all adult tree observations within 1° latitude of this minimum observation as our southern tree edge. Using this median value reduces excess variability associated with outlier points. To determine the seedling southern edge, we determine the median latitude of all seedling observations in this same 1° grid cell as well as any seedling observations further south than the adult tree minimum. If no seedlings were observed within or south of a particular grid cell, we took the absolute minimum seedling observation for that longitudinal band as the seedling southern edge. For the northern edge, we performed a similar analysis, but took into account any seedling observations north (rather than south) of a grid cell. If no seedlings were observed in or north of a particular grid cell, we took the absolute maximum seedling observation for that longitudinal band as the seedling northern edge. We then subtracted the latitudinal value determined for the seedling range edge from that determined for the tree range edge. A positive value at the leading edge represents range expansion, and at the trailing edge represents range contraction. This analysis was performed in 1° longitudinal bands ranging from 67° to 94° W. We determined the mean LDD across all bands, as well as the 95% confidence interval using longitudinal bands as samples. These calculations are visualized in Appendix A: Fig. A1. For the leading edge, we restricted analysis to species having northern range boundaries within the FIA sampling extent.

We determined the spatial velocity of temperature change at the southern and northern range boundary for each species in each longitudinal band using the data from Zhu et al. (2012). We determined the mean temperature velocity across all bands per species, and then subtracted this estimate of temperature velocity from the estimate of biotic velocity (i.e., LDD) to create a metric of climate tracking. At the northern edge, a positive value indicated that northward range expansion exceeds the rate of temperature change, while a negative value indicated ranges that lag behind temperatures. At the southern edge, a positive value indicated that northward contraction of seedlings relative to adult trees has occurred more rapidly than the rate of warming, while a negative value indicated the persistence of recruitment in the face of warming temperatures. These interpretations did not hold when temperature velocity is negative (i.e., to the south, or cooling), and so we restricted our analyses to those species experiencing net warming at a given range edge. Our metric of temperature velocity was on a century timeframe. Our metric of biotic "velocity" came from non-temporal data, but likely integrates responses over several decades for most species. Thus, absolute values of the biotic–climatic velocity metric should not be interpreted strongly; nevertheless, relative differences among species are informative.

We used Brundrett (1991) and Wang and Qiu (2006) to assign taxa to mycorrhizal types. For families listed as having variable mycorrhizal associations, we used additional literature searches to assign genera to a mycorrhizal type. We excluded species with ericoid mycorrhizae (one species, *Oxydendron arboreum*), and 10 species that are routinely dually colonized by both AM and EM fungi (*Alnus*, *Populus*, and *Salix* species). For each remaining species we searched the Kew Seed Information Database and the USDA Plants database for seed mass, with preference given to the Kew Database (databases *available online*).[7,8] We obtained shade tolerance categories (very intolerant, intolerant, intermediate, tolerant, and very tolerant) from the USFS Silvics manual (Burns and Honkala 1990) and the USDA Plants database, with preference given to the USFS Silvics manual. Shade tolerance categories were converted to an ordinal scale (1–5) for analysis. We were left with 49 AM and 48 EM tree species for analysis of southern ranges, and a set of 41 AM and 43 EM species for northern range analysis. We obtained a phylogenetic tree for the 97 species from the Phylocom website using

[6] http://dataneotomadb.org

[7] http://data.kew.org/sid/

[8] http://plants.usda.gov

TABLE 1. Phylogenetic least squares linear models of biotic vs. climatic velocity at trailing and leading edges during historical and contemporary climate change.

Biotic vs. climatic velocity, Younger Dryas (12 000–10 000 yr BP)	Southern (trailing) edge			Northern (leading) edge		
	Estimate	LR	*P*	Estimate	LR	*P*
Historical data set						
Phylogenetic correlation (Pagel)	−0.223	0.784	0.376	0.544	1.426	0.233
Fixed effects†						
Mycorrhizal type	**−3.340**	**3.998**	**0.046**	−0.141	0.912	0.340
Shade tolerance	**2.038**	**5.311**	**0.021**	**0.163**	**5.221**	**0.022**
ln(seed mass)	−0.329	1.297	0.255	0.007	0.075	0.784
Contemporary data set						
Phylogenetic correlation (Pagel)	0.316	2.197	0.138	**0.526**	**6.518**	**0.011**
Fixed effects†						
Mycorrhizal type	**−25.604**	**4.437**	**0.035**	−9.009	0.306	0.580
Shade tolerance	−2.505	0.380	0.538	1.087	0.048	0.827
ln(seed mass)	**4.524**	**5.512**	**0.019**	**6.401**	**4.265**	**0.039**

Notes: LR, likelihood ratio. Bold text indicates significant outcomes evaluated at $P < 0.05$.
† Fixed effects tested by model comparison using maximum likelihood and λ (Pagel correlation parameter) fixed at 0 (southern edge) or 0.544 (northern edge) in the historical data set, and 0.316 (southern edge) or 0.526 (northern edge) in the contemporary data set.

the megatree from Smith et al. (2011). For species not present in the tree, we substituted a con-generic species and added our species as a polytomy.

For the analysis of historical data, we excluded two dually colonized (*Alnus* and *Salix*) and one non-mycorrhizal (*Sarcobatus*) genera. To obtain estimates of seed size and shade tolerance for the genera, we took the weighted average of these traits for all members of the genus present in the FIA dataset, weighted by the sum of basal diameter for each species. We pruned the phylogenetic tree to include a single representative of each of the 18 genera (or sub-genera, for *Pinus*) present in the 12 000 to 10 000 BP time window.

We used phylogenetic least squares with a Pagel correlation structure to test whether the difference between biotic and climatic velocities differed between AM and EM genera and species at both the northern and southern range edges (Freckleton et al. 2002), using the nlme and ape packages in R (Paradis et al. 2004, Pinheiro et al. 2008). Results were qualitatively similar using phylogenetic correlation structures defined by alternative models of trait evolution (including Brownian and non-Brownian models; Appendix B: Table B1). Models included shade tolerance rank and seed size (log-transformed) to control for other functional traits that may covary with mycorrhizal type. We present *P* values derived from likelihood ratio (LR) tests for all terms in this model, including the phylogenetic correlation structure. We first fit a model with or without the phylogenetic error structure using restricted estimate maximum likelihood (REML), and performed a LR test. We then fixed the λ parameter in the Pagel correlation structure at its REML estimated value, fit models with or without each fixed effect term separately using maximum likelihood, and used LR tests to determine the significance of each term. For southern ranges in the historical dataset, the estimated λ parameter in the Pagel correlation structure was negative and did not significantly improve model fit; therefore, we present results from a model with no phylogenetic correction. Results for models without phylogenetic correction for the other datasets are presented in Appendix B (Tables B2 and B4). Samples were weighted by the 95% confidence interval in their LDD. To test the effect of excluding dually colonized species, we ran an identical set of models with three mycorrhizal categories (AM species, EM species, and dually colonized). Dually colonized species tended to show results intermediate to the purely AM species or EM species (Appendix B: Tables B3 and B4).

RESULTS AND DISCUSSION

Contrary to our predictions, we did not find a significant difference in rates of northward range expansion relative to climate velocity between AM or EM genera and species in either the contemporary or historical datasets (Table 1). In the historical dataset, the temporal resolution may be too coarse to detect a pattern of mutualist limitation, which relies on mismatches in migration rates between trees and fungi. Even if such mismatches occurred, they would likely be resolved within the 2000 year time windows analyzed. In the contemporary dataset, the majority of species of both mycorrhizal types showed stable or contracting northward range boundaries, consistent with the analysis of Zhu et al. (2012), indicating that either the current degree of climate change has not been sufficient to result in range expansion, or that expansion is currently constrained by factors independent of mycorrhizal type. Thus, our power to detect differences in leading edge range expansion between the mycorrhizal types, as might be predicted by greater potential for symbiont limitation in EM trees, was low.

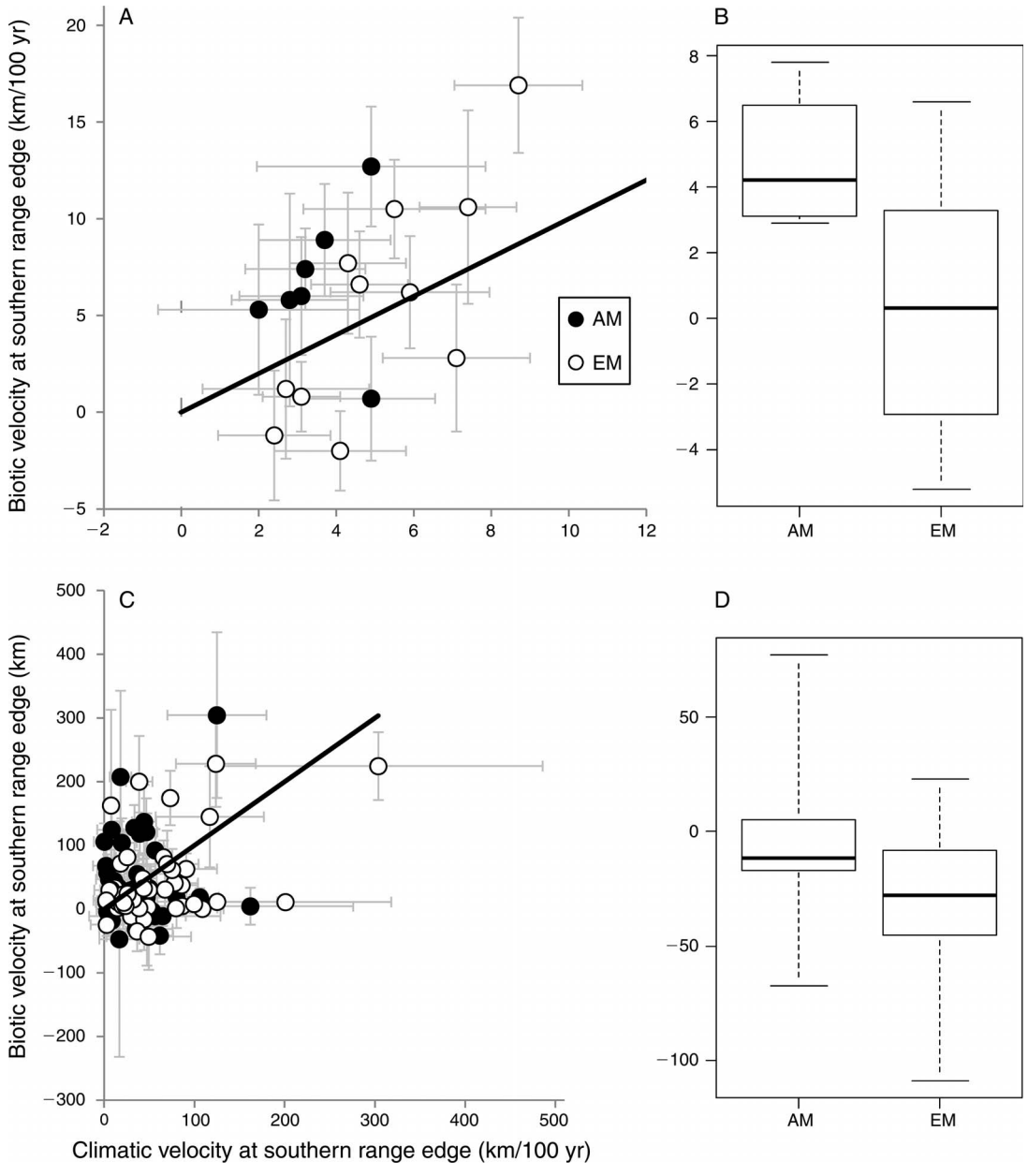

FIG. 1. Biotic vs. climatic velocity at the southern range edge in response to (A, B) past or (C, D) contemporary climate change. (A) Biotic velocity is measured as the spatial displacement of the southern 5% of the core range for each genus during the Younger Dryas warming, 12 000 and 10 000 yr BP, for AM tree taxa (black circles) and EM tree taxa (white circles). Climate velocity in (A) is measured as the distance between climate analogs based on 12 temperature and precipitation variables over a 2000-year time window, then divided by 20 to give a velocity per 100 yr. (C) Biotic velocity is measured as the difference in latitude of seedling vs. adult tree distributions for AM tree taxa (black circles) and EM tree taxa (white circles). Climate velocity in (C) is measured as the spatial displacement of temperature over the last 100 years. Solid lines show a 1:1 relationship between biotic velocity and climate velocity. Symbols below the 1:1 line indicate reduced northward contraction relative to the rate of climate change at their southern edge. (B and D) Box-and-whisker plots displaying the median (solid line), 25th and 75th percentiles (box), and 5th and 95th percentiles (whiskers) in the difference between biotic and climate velocities for AM and EM tree taxa. Percentiles are weighted by within species confidence intervals.

Nevertheless, we found a strikingly consistent pattern for EM tree genera and species to show reduced rates of contraction of their trailing edge in the face of warming climate in both the historical and contemporary datasets (Fig. 1, Table 1); this was consistent with our hypothesis that the EM symbiosis may allow broader tolerance to a novel climate. In both datasets our estimates of biotic velocities are generally positive, indicating northward

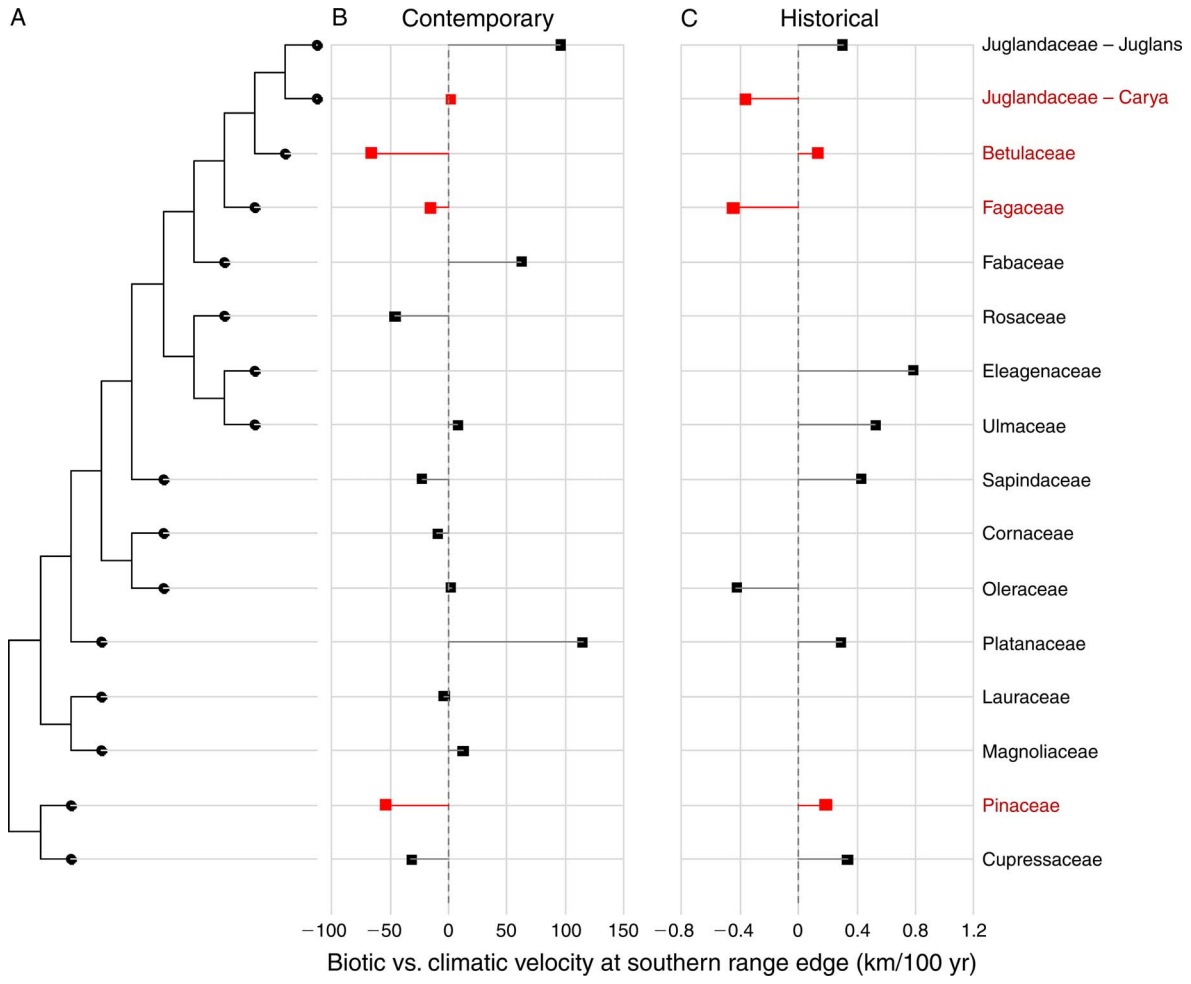

FIG. 2. (A) Phylogenetic relationships among plant families included in the contemporary and historical datasets. For clarity, plant families in the contemporary dataset that were represented by a single species are not shown. Family mean values of biotic vs. climatic velocities at the southern range edge are shown for the (B) contemporary and (C) historical data sets. Negative values indicate a range contraction that is slower than climate change, while positive values indicate a range contraction that is faster than climate change. Red symbols and text indicate EM plant families, black symbols and text indicate AM families. One family, Juglandanceae, contains both AM genera (Juglans) and EM genera (Carya) that are plotted separately.

contraction at the trailing edge (Fig. 1). On average, EM taxa trailing edges contracted at the same (historical dataset) or slower (contemporary dataset) rates compared to climate, while AM taxa trailing edges contracted at faster (historical dataset) or similar (contemporary dataset) rates as climate (Fig. 1 B, D). These results were qualitatively similar when using alternative metrics for biotic velocities in the contemporary dataset (Appendix B). In both datasets there is a general pattern of reduced southern biotic velocity relative to climate velocity in EM clades compared to related AM clades for both angiosperms and gymnosperms (Fig. 2).

Like most studies of its kind, this analysis of distributional patterns lacks mechanistic detail. Associations between species traits and distribution patterns may occur for a variety of causal reasons, including shared correlations with unmeasured traits or other factors. In our case, we considered two traits generally hypothesized to play a role in tree responsiveness to climate: seed size (a proxy for dispersal ability) and shade tolerance (a proxy for successional stage and tolerance to competition). In general we found these two traits to be inconsistent predictors of range dynamics, having effects in either the historical or contemporary datasets, but not both. Shade tolerant genera tended to expand at their northern edge, but also contract at their southern edge, more rapidly relative to climate velocity in the historical dataset. Larger seeds were positively correlated with increased southern contraction in the contemporary data set (Table 1). However, they were also correlated with reduced rates of contraction at the northern range edge (note that very few species showed actual northward expansion, and large seeded species were not more likely to show expansion than small seeded species). Additionally, we used phylogenetic

analyses to control for the effect of shared, unmeasured traits among related species (to the degree that phylogenetic similarity is a reasonable proxy for trait similarity). However, including phylogenetic error structures rarely improved model fit (only for northern range dynamics in the contemporary dataset), suggesting that variance in climate responsiveness is only weakly conserved phylogenetically, once we controlled for mycorrhizal and other functional traits.

Understanding whether a particular species will respond to a changing climate via adaptation, acclimation, or migration (or just go extinct) is a vitally important but inherently challenging endeavor. Species traits may provide a useful tool to help predict individual species responses, but to date the search for informative traits has met with variable success (Angert et al. 2011, Buckley and Kingsolver 2012). This may reflect the reality that no species interacts with its environment in a vacuum, but rather as part of a complex community, as shown by simulations by Urban et al. (2012). If interactions among species (across and within trophic levels) play an important role in mediating a given species' response to changing climate, then traits controlling these interactions may provide additional predictive power. We take a coarse first step towards this approach by comparing responses of temperate tree species that associate with arbuscular vs. ectomycorrhizal fungal symbionts, since this important interaction can mediate host tree responses to numerous stressors. We found that this simple, qualitative trait was consistently associated with tolerance to novel climates at the species' trailing range edge during both historical and contemporary climate change.

The majority of research on distributional responses to climate change, including those searching for explanatory species traits, has focused primarily on rates of range expansion at leading edges. However, whether a species will be able to persist in a changing world will be determined not only by its ability to track climate in space, but also by its ability to tolerate novel climates in place. Greater tolerance to novel climates at trailing edges can provide a buffer against range-wide extinction even if dispersal barriers slow rates of expansion at the leading edge. Our finding that variation in symbiotic relationships affects rates of range contraction suggests that more detailed, mechanistic investigations of species interactions, especially at trailing edges experiencing stressful and novel climates, may prove valuable in understanding variation in climate "winners" and "losers."

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Literature Cited

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters 14:677–689.

Averill, C., B. L. Turner, and A. C. Finzi. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505:543–545.

Bingham, M. A., and S. Simard. 2012. Ectomycorrhizal networks of *Pseudotsuga menziesii* var. *glauca* trees facilitate establishment of conspecific seedlings under drought. Ecosystems 15:188–199.

Booth, M. G., and J. D. Hoeksema. 2010. Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. Ecology 91:2294–2302.

Brundrett, M. 1991. Mycorrhizas in natural ecosystems. Advances in Ecological Research 21:171–313.

Buckley, L. B., and J. G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. Annual Review of Ecology, Evolution, and Systematics 43:205–226.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA

Chen, I. C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid rangshifts of species associated with high levels of climate warming. Science 333:1024–1026.

Courty, P. E., M. Buee, A. G. Diedhiou, P. Frey-Klett, F. Le Tacon, F. Rineau, M. P. Turpault, S. Uroz, and J. Garbaye. 2010. The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. Soil Biology and Biochemistry 42:679–698.

Engelkes, T., E. Morrien, K. J. F. Verhoeven, T. M. Bezemer, A. Biere, J. A. Harvey, L. M. McIntyre, W. L. M. Tamis, and W. H. van der Putten. 2008. Successful range-expanding plants experience less above-ground and below-ground enemy impact. Nature 456:946–948.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Jones, A. M., R. Berkelmans, M. J. H. van Oppen, J. C. Mieog, and W. Sinclair. 2008. A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. Proceedings of the Royal Society B 275:1359–1365.

Kivlin, S. N., S. M. Emery, and J. A. Rudgers. 2013. Fungal symbionts alter plant responses to global change. American Journal of Botany 100:1445–1457.

Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions 8:1535–1545.

Merrild, M. P., P. Ambus, S. Rosendahl, and I. Jakobsen. 2013. Common arbuscular mycorrhizal networks amplify competition for phosphorus between seedlings and established plants. New Phytologist 200:229–240.

Nunez, M. A., T. R. Horton, and D. Simberloff. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. Ecology 90:2352–2359.

Ordonez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16000 years in eastern North America. Ecology Letters 16:773–781.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010. Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. Ecology 91: 3631–3640.

Phillips, R. P., E. Brzostek, and M. G. Midgley. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytologist 199:41–51.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. team.2008. nlme: Linear and nonlinear mixed effects models. R package version 3.1-89. http://CRAN.R-project.org/package=nlme

Pringle, A., J. D. Bever, M. Gardes, J. L. Parrent, M. C. Rillig, and J. N. Klironomos. 2009. Mycorrhizal symbioses and plant invasions. Annual Review of Ecology, Evolution, and Systematics 40:699–715.

Read, D. J., and J. Perez-Moreno. 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytologist 157:475–492.

Smith, S. A., J. M. Beaulieu, A. Stamatakis, and M. J. Donoghue. 2011. Understanding angiosperm diversification using small and large phylogenetic trees. American Journal of Botany 98:404–414.

Smith, S. E., and D. J. Read. 2008. Mycorrhizal symbiosis. Academic Press, London, UK.

Svenning, J.-C., et al. 2014. The influence of interspecific interactions on species range expansion rates. Ecography 37(12):1198–1209.

Svenning, J. C., and B. Sandel. 2013. Disequilibrum vegetation dynamics under future climate change. American Journal of Botany 100:1266–1286.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B 279: 2072–2080.

van der Heijden, M. G. A., and T. R. Horton. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. Journal of Ecology 97: 1139–1150.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society B 365:2025–2034.

Wang, B., and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan, New York, New York, USA.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18:1042–1052.

Supplemental Material

Ecological Archives

Appendices A and B and the Supplement are available online: http://dx.doi.org/10.1890/14-2419.1.sm